

TAXONOMIC STUDIES OF DWARF MISTLETOES (*ARCEUTHOBIMUM* SPP.)
PARASITIZING *PINUS STROBIFORMIS*

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ABSTRACT.— Analysis of morphological characters of *Arceuthobium apachecum* and *A. blumeri* indicates there are several geographically consistent differences between these taxa, which supports their current classification at the specific level. Shoot height and perianth lobe number exhibited considerable geographic variation, and some morphological characters examined were continuous. Peak flowering and seed dispersal periods for these species differed slightly. Altitudinal, seasonal, and latitudinal variations in flowering and seed dispersal were detected and may be responsible for the differences in phenology between these taxa.

Dwarf mistletoes (*Arceuthobium* spp.) are the most serious disease agents of conifers in the southwestern United States. Many of the North American species of *Arceuthobium* were described by Engelmann in the 1800s (Gray 1850, Watson 1880). Gill (1935) prepared the first comprehensive monograph of the genus, in which he reduced several previously recognized fall-flowering species to host forms of *A. campylopodum* Engelm. Gill designated forms of *A. campylopodum* exclusively on the basis of host relationships because he recognized few morphological differences between these taxa. In Gill's system *A. campylopodum* Engelm. forma *blumeri* (Engelm.) Gill encompasses the dwarf mistletoes that parasitize sugar pine (*Pinus lambertiana* Dougl.) and western white pine (*Pinus monticola* Dougl.) in California and Oregon and those that parasitize southwestern white pine (*Pinus strobiformis* Engelm.) in Arizona and New Mexico. Hawksworth and Wiens (1965, 1970, 1972) described several new species of *Arceuthobium* from Mexico and the Western United States and reported that many of Gill's host forms could be distinguished morphologically and physiologically, including *A. campylopodum* f. *blumeri* and f. *cyanocarpum* (A. Nelson) Gill. They separated f. *blumeri* into three species, *A. californicum* Hawksw. & Wiens, *A. apachecum* Hawksw. & Wiens, and *A. blumeri* A. Nelson, based on morphology, phenology, and geographic distribution. *Arceuthobium apachecum* exclusively para-

sitizes *Pinus strobiformis* and is distributed from the Santa Rita and Chiricahua Mountains of southern Arizona north to east central Arizona and west central New Mexico, with one population known from northern Coahuila, Mexico (Hawksworth and Wiens 1972, Mathiasen 1979). *Arceuthobium blumeri* parasitizes *Pinus strobiformis* and *Pinus ayacahuite* var. *brachyptera* Shaw (Mexican white pine) and is distributed from the Huachuca Mountains, Arizona south through the Sierra Madre Occidental to southern Durango, Mexico, with one population known from Nuevo León, Mexico (Hawksworth and Wiens 1972, Mathiasen 1979). *Arceuthobium apachecum* and *A. blumeri* are morphologically similar, but can be distinguished by shoot color, shoot height, growth habit, and number of perianth lobes of staminate flowers (Hawksworth and Wiens 1972). Few data, however, were available on the phenology of these species (Hawksworth and Wiens 1972), and because of their morphological similarity their specific status has been questioned (Kuijt 1973). This study was undertaken to provide more information on the morphological and physiological characters of these two taxa.

MATERIALS AND METHODS

Measurements and observations of morphological characters were made on 21 populations of *A. apachecum* and 18 populations of *A. blumeri* distributed throughout their geographic ranges. Specimens examined were

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collected by the author in 1975 and 1976 or were previously deposited at the U.S. Forest Service, Forest Pathology Herbarium, Fort Collins, Colorado (FPF) or the University of Arizona Herbarium, Tucson, Arizona (ARIZ). The specimens examined represent essentially all the material that has been collected for these species. Measurements and observations were made for the following morphological characters: staminate and pistillate shoot height, pistillate shoot basal diameter, staminate and pistillate shoot color, and shoot growth habit (all measurements and observations for dominant shoots of nonsystemic infections only); length and width of staminate spikes in summer; staminate flower diameter; perianth lobe number and color; mature fruit length, width, and color; mature seed length, width, and color. The original measurements of shoot height made for these taxa by Hawksworth and Wiens (1972) were available and were included in obtaining mean, maximum, and minimum values for this character.

Observations of flowering and seed dispersal for both species were made in Arizona and New Mexico in the summer and fall of 1973 through 1976. The species, location, elevation, and date were recorded for each field observation, and flowering and seed dispersal were each rated as not started, started but not near peak, near peak, past peak but not completed, and completed. Phenological data were examined by weekly periods for all observations from 1 July through 2 November to determine the approximate periods of flowering and seed dispersal for both species.

RESULTS

Mean heights of staminate and pistillate shoots of *A. blumeri* were approximately 1.5 cm greater than those of *A. apacheicum*, and maximum shoot heights of *A. blumeri* were also twice those of *A. apacheicum* (Table 1). Nevertheless, analysis of shoot heights for these taxa using the method for comparing two sample means described by Cochran and Cox (1957) for samples with unpaired observations and unequal variance indicates that the differences are not significant at the 5 percent level. Analysis of separate populations from east central Arizona to southern Durango, Mexico, indicates that shoots are smallest for the northern populations of both species and largest for the southern populations (Table 2). In addition, shoot heights are approximately the same for these taxa in southern Arizona (Table 2). Shoots of *A. blumeri* vary in color from light green to straw or gray, and those of *A. apacheicum* vary from yellow-green to blue or reddish. Both species parasitize *Pinus strobiformis*, but their growth habit is different on this host. Shoots of *A. apacheicum* are consistently densely clustered around the host branch and may even completely obscure the branch. Shoots of *A. blumeri* are more scattered and are rarely densely clustered on a branch.

Lateral staminate spikes are larger for *A. blumeri* (means 12 × 2 mm) than for *A. apacheicum* (means 7 × 1 mm). The mean diameter of staminate flowers of *A. blumeri* is larger than that of *A. apacheicum*, but their

TABLE 1. Comparison of selected morphological characters of *Arceuthobium apacheicum* and *Arceuthobium blumeri*.

CHARACTER	<i>A. apacheicum</i>					<i>A. blumeri</i>				
	Mean	Max.	Min.	No. populations sampled	No. measured	Mean	Max.	Min.	No. populations sampled	No. measured
Shoot height (cm)										
Pistillate	4.7	9.5	2.5	21	254	6.1	18.0	3.0	18	218
Staminate	3.4	7.5	2.0	16	194	5.0	16.0	2.0	14	107
Shoot basal diameter (mm) (Pistillate)	1.7	4.4	0.8	21	234	2.0	3.4	1.2	18	193
Staminate flower diameter (mm)	2.9	4.2	2.2	10	296	3.2	4.4	2.0	6	146
Mature fruit (mm)										
Length	3.2	4.0	2.6	14	310	3.5	4.0	2.0	10	175
Width	1.9	2.4	1.4	14	310	2.0	2.4	1.6	10	175

size range is approximately the same (Table 1). Perianth lobe dimensions are similar also, but their color varies. In *A. apacheicum* the perianth lobes are the same color as the male shoots, but in *A. blumeri* they are darker. These species also differ in the number of perianth lobes. *Arceuthobium apacheicum* is predominantly 3-merous (65 percent), commonly 4-merous (33 percent), and rarely 5-merous (2 percent); *A. blumeri* is predominantly 4-merous (53 percent), less commonly 3 or 5-merous (31 percent and 15 percent, respectively), and rarely 6-merous (1 percent). Comparison of perianth lobe number in separate populations from east central Arizona to southern Durango, Mexico, indicates that 3-merous staminate flowers predominate in the northern populations of *A. apacheicum* and gradually change until 4-

merous flowers predominate in most of the southern populations of this species (Table 3). Four-merous flowers predominate in the most northern populations of *A. blumeri*, but the few counts made for this species in Mexico indicate that 3-merous flowers may predominate in the southern populations. Six-merous flowers were found only in the Arizona population of *A. blumeri* (Huachuca Mountains).

Fruits are approximately the same size for both species (Table 1). Mean dimensions of mature seed were similar also (2.6×1.1 mm for *A. blumeri* and 2.3×1.0 mm for *A. apacheicum*), but seeds of *A. blumeri* are dark green and those of *A. apacheicum* are light green. Seeds from Mexican populations of *A. blumeri* were not available for examination, however.

TABLE 2. Geographic variation in shoot height of *Arceuthobium apacheicum* and *Arceuthobium blumeri*.

LOCATION (Latitude)	Pistillate (cm)		Staminate (cm)		No. populations sampled
	Mean	Max.	Mean	Max.	
<i>A. apacheicum</i>					
White Mountains, Arizona	4.0	5.0	3.1	4.3	6
Mogollon Mountains, New Mexico (33°20'–34°10'N)					
Mangas Mountains, New Mexico (34°5'N)	4.1	5.0	2.0	3.0	2
Magdalena and San Mateo Mountains, New Mexico (34°N)	4.7	6.0	3.7	4.5	2
Capitan Mountains, New Mexico (33°30'N)	4.2	5.5	2.0	4.0	2
Pinaleno Mountains, Arizona (32°30'N)	4.2	5.0	3.7	4.4	2
Santa Catalina Mountains, Arizona (32°25'N)	5.8	7.5	4.3	6.1	2
Chiricahua Mountains, Arizona (31°50'N)	4.9	6.0	4.2	5.0	2
Santa Rita Mountains, Arizona (31°40'N)	6.3	9.5	4.9	7.5	3
<i>A. blumeri</i>					
Huachuca Mountains, Arizona (31°30'N)	6.4	8.5	4.2	8.0	3
Sierra de Ajos, Sonora, Mexico (30°30'N)	6.0	7.5	—	—	1
Chihuahua, Mexico (26°30'–29°30'N)	5.9	11.5	4.7	8.0	8
Durango, Mexico (23°–26°N)	8.0	18.0	7.6	16.0	5

Arceuthobium blumeri consistently flowers earlier than *A. apachecum* (Fig. 1), but one of the most southern populations of *A. apachecum* (Santa Rita Mountains, Arizona) flowers at approximately the same time as the most northern population of *A. blumeri* (Huachuca Mountains, Arizona). These populations are separated by almost 40 miles. *Arceuthobium apachecum* disperses seed somewhat earlier than *A. blumeri* (Fig. 1). Data on the flowering and seed dispersal periods of *A. blumeri* populations in Mexico are still inadequate, but they are evidently similar to the *A. blumeri* population in Arizona (Hawksworth and Wiens 1972). Both species show altitudinal variation in flowering and seed dispersal. Lower populations flower earlier than higher populations in the same mountain ranges in southern Arizona and the reverse is true for seed dispersal. Flowering of *A. apachecum* begins as early as mid-August in the northern populations of this species, but does not start until early September in the southern populations observed. Annual climatic variations also influence the phenology of these species. Seed dispersal starts later in years with a late fall.

DISCUSSION

Arceuthobium apachecum and *A. blumeri* are morphologically similar, but differ in color of staminate and pistillate shoots, growth habit, dimensions of lateral staminate spikes, color of perianth lobes, and seed color. Shoot height and number of perianth lobes appear to be discontinuous characters also, but analysis of different populations indicates that considerable geographic variation occurs in these characters. Although mean shoot heights are different for these species, shoots are shortest in the northern populations of *A. apachecum*, tallest in the southern populations of *A. blumeri*, and approximately the same near the geographic boundary between these taxa in southern Arizona. Variation in the number of perianth lobes appears to follow a geographic pattern also, but more information is needed for Mexican populations of *A. blumeri*. Six-merous flowers are only known for *A. blumeri*, however.

Periods of flowering and seed dispersal for *A. apachecum* and *A. blumeri* are slightly different, although one population of *A. apachecum* does flower at approximately the same

TABLE 3. Geographic variation in number of perianth lobes of *Arceuthobium apachecum* and *Arceuthobium blumeri*.

LOCATION (Latitude)	3	4	5	6	No. populations sampled	No. measured
<i>A. apachecum</i> (%)						
White Mountains, Arizona (33°20'-34°10'N)	81	19	0	0	6	390
Pinaleno Mountains, Arizona (32°30'N)	68	30	2	0	2	50
Chiricahua Mountains, Arizona (31°50'N)	42	54	4	0	2	50
Santa Catalina Mountains, Arizona (32°25'N)	54	42	4	0	2	480
Santa Rita Mountains, Arizona (31°40'N)	43	48	8	0	3	500
<i>A. blumeri</i> (%)						
Huachuca Mountains, Arizona (31°30'N)	30	53	16	1	3	700
Chihuahua, Mexico (26°30'-29°30'N)	40	58	2	0	5	50
Durango, Mexico (23°-26°N)	55	44	1	0	5	100

time as *A. blumeri* in Arizona. Latitudinal variation, however, may influence these differences in flowering and seed dispersal. *Arceuthobium blumeri* has a more southerly range and flowers before *A. apacheicum*, but disperses seed slightly later. This pattern is evident in the elevational variation observed for both taxa where lower populations begin flowering before higher populations in the same mountain ranges, but disperse seed sooner at the higher elevations. Scharpf (1965) reported a similar altitudinal relationship for flowering and seed dispersal of *A. abietinum* Engelm. ex Munz in California. Northern populations of *A. apacheicum* start seed dispersal before southern populations of this species in Arizona, which also suggests that latitude influences this character. Therefore, the slight differences in the flowering and seed dispersal periods of these species, and possibly other fall-flowering species in the Series *Campylopoda* Hawksw. & Wiens (Hawksworth and Wiens 1970, 1972) may be a result of climatic fluctuations, possibly temperature variation (Scharpf 1965), associated with latitudinal, altitudinal, or seasonal differences. Variation in the flowering and seed dispersal periods of dwarf mistletoes is com-

plex and deserves more study before phenology can play an important role in the classification of fall-flowering species of *Arceuthobium*.

Environmental factors may influence other physiological characters of dwarf mistletoes. The consistent inducement of witches' brooms by *A. apacheicum* and the rare inducement of brooms by *A. blumeri* was considered as a taxonomically significant discontinuity between these species by Hawksworth and Wiens (1972). Some populations of both species rarely cause brooms at lower elevations, however, but frequently cause brooms at higher elevations (Mathiasen 1979). The reason for this apparent relationship between witches' broom formation and elevation is unknown, but the rare inducement of brooms by *A. blumeri* reported by Hawksworth and Wiens is not typical of that species.

Geographic variation in morphological and physiological characters of dwarf mistletoes may be influenced by variation in their host population as well as parasitism of different hosts. Shoot height of dwarf mistletoes is directly related to variation in host vigor (Hawksworth 1960, Hawksworth and Wiens

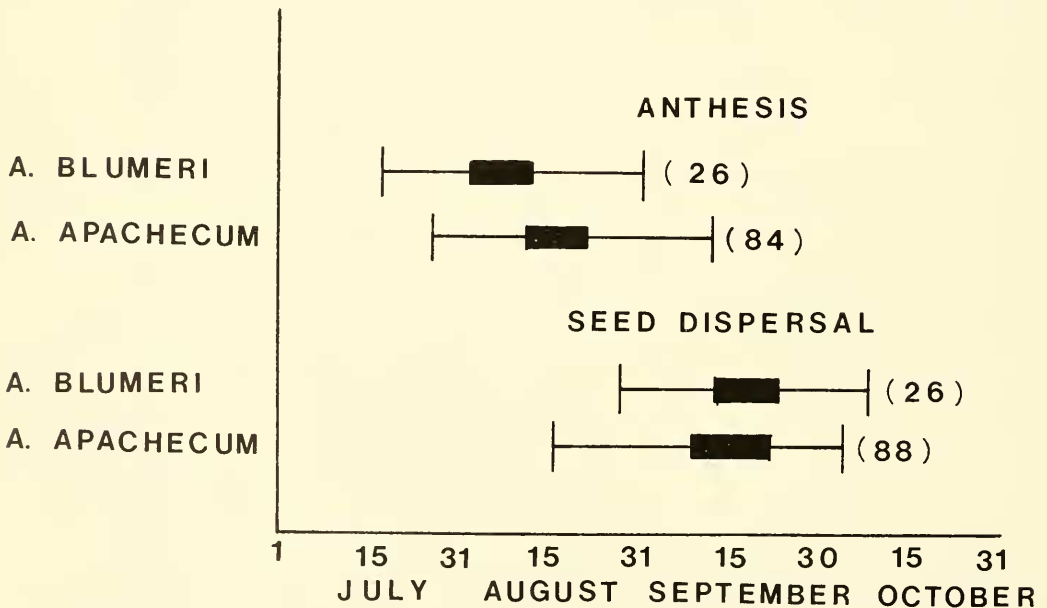


Fig. 1. Approximate periods of anthesis and seed dispersal of *Arceuthobium blumeri* and *Arceuthobium apacheicum*. Peak periods are shown by solid bars. Number of observations are in parentheses.

1972) and may itself influence other characters of a dwarf mistletoe. The southern populations of *A. blumeri* parasitize *Pinus ayacahuite*, which is one of the largest pines in Mexico (Loock 1950, Mathiasen 1979). *Pinus ayacahuite* commonly occurs in moist localities, with deep, well-drained soils that are conducive to maintaining a vigorous growth rate (Loock 1950). Therefore, the large shoot heights found in the southern populations of *A. blumeri* may be related to the parasitism of a more vigorous host population. The taxonomic relationships between *P. ayacahuite* and *P. strobiformis* are uncertain. Morphological and physiological variation has been reported in different populations of *P. strobiformis* (Andresen and Steinhoff 1971) and the various taxonomic treatments of this species in different parts of its range suggest that it is quite variable (Steinhoff and Andresen 1971). Critchfield and Little (1966) considered all white pine populations from Durango, Mexico, northward to the southwestern United States to be *P. strobiformis*. Nevertheless, other investigators believe that many of the white pine populations in northern Mexico are typical of *P. ayacahuite* (Martinez 1948, Loock 1950, Mathiasen 1979). Further taxonomic studies of the white pine populations represented in the southwestern United States and northern Mexico are needed and may provide additional information concerning the relationships between *A. blumeri* and *A. apachecum*.

Hawksworth and Wiens (1972) originally considered that the dwarf mistletoes parasitizing *P. strobiformis* might represent a single variable taxon. They finally concluded that *A. apachecum* and *A. blumeri* warranted separate taxonomic status at the specific level, because they believed the morphological and physiological differences they detected between these taxa were geographically consistent. Hawksworth and Wiens (1972) considered two criteria as the most important factors in delimiting species of *Arceuthobium*: (1) species maintain their morphological integrity when parasitizing species other than their principal hosts, and (2) species of *Arceuthobium* are often sympatric but do not show evidence of hybridization. It is not known if *A. apachecum* and *A. blumeri* meet these criteria because they are not sympatric

and do not parasitize any species other than their principal hosts (Hawksworth and Wiens 1972, Mathiasen 1979). Hawksworth and Wiens (1972), however, reported that these taxa maintain their morphological integrity when grown under common greenhouse conditions. In addition, chemical analysis of the shoots of these species has shown there are consistent differences in their phenolic chemistry (Hawksworth and Wiens 1972, Crawford and Hawksworth 1979). Artificial hybridization of *A. apachecum* and *A. blumeri* has been attempted, but the results were inconclusive (Mathiasen, unpubl. ms.). Crosses between *A. apachecum* (staminate) and *A. blumeri* (pistillate) were destroyed by a wild-fire in the Huachuca Mountains, Arizona, in 1977 before results could be assessed. Crosses between *A. blumeri* (staminate) and *A. apachecum* (pistillate) in the Santa Catalina Mountains, Arizona, resulted in no successful fruit set, but the control crosses (*A. apachecum* [staminate] × *A. apachecum* [pistillate]) yielded very poor fruit set. These investigations must be repeated before their results can be considered as evidence these species are reproductively incompatible.

Although geographic variation occurs in some of the morphological and physiological characters used by Hawksworth and Wiens to delimit *A. apachecum* and *A. blumeri*, the results of this study indicate there are several geographically consistent morphological discontinuities between these taxa. I believe these morphological differences are taxonomically significant and suggest that these dwarf mistletoes should be given separate taxonomic recognition. Nevertheless, these populations may represent intermediate stages of gradual evolutionary divergence, and perhaps their recognition at the sub-specific level would be more representative of their natural relationship.

Hawksworth and Wiens (1972) defined subspecies of *Arceuthobium* as "geographically restricted populations, delimited by relatively few but consistent variations." The dwarf mistletoe populations parasitizing *Pinus strobiformis* appear to more closely conform to these criteria than those used by Hawksworth and Wiens to define species of *Arceuthobium*. Examination of the discontinuities separating currently recognized

subspecies of *Arceuthobium* (Hawksworth and Wiens 1970, 1972, 1977) indicates there are more morphological and physiological differences between these taxa than between *A. apacheicum* and *A. blumeri*. Several species in the Series *Campylopora*, however, including *A. apacheicum* and *A. blumeri*, are delimited by relatively few morphological and physiological differences, so the classification of taxa in this series is relatively consistent. Because species and subspecies of *Arceuthobium* differ only in the number of discontinuities between them (Hawksworth and Wiens 1972), the elevation of currently recognized subspecies to specific rank or the separation of some species into subspecies would alleviate the apparent inconsistencies I feel exist in the present classification of *Arceuthobium*. Consistency in the classification of a group is desirable and changes in the rank of taxa for motives of consistency or for achieving a more balanced natural classification are justified (Davis and Heywood 1963). Isozyme analyses and additional field studies of dwarf mistletoe populations in Mexico and the western United States are in progress, and the results may provide evidence that changes in the rank of some taxa would create a more natural and consistent classification of the genus (F. G. Hawksworth and Dan Nikrent, pers. comm., 1981). Therefore, I do not feel that a change in the rank of *A. apacheicum* or *A. blumeri* should be considered until additional information is available concerning their natural relationships and their relationship with other species in the Series *Campylopora*.

Stability in the classification of such an economically important group as *Arceuthobium* is desirable; yet it is doubtful that this can be achieved in the near future because little is known about the ranges and natural relationships of the recently discovered Mexican and Central American species (Hawksworth and Wiens 1972, 1977, 1980). More than one-half of the taxa now recognized have been described in the last 10 to 15 years, so much critical work on the entire genus will be required before a more stable classification of *Arceuthobium* can be achieved.

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